

Rhesus Monkeys Attribute Perceptions to Others

Jonathan I. Flombaum* and Laurie R. Santos

Department of Psychology

Yale University

New Haven, CT 06520

Summary

Paramount among human cognitive abilities is the capacity to reason about what others think, want, and see—a capacity referred to as a theory of mind (ToM). Despite its importance in human cognition, the extent to which other primates share human ToM capacities has for decades remained a mystery. To date, primates [1, 2] have performed poorly in behavioral tasks that require ToM abilities, despite the fact that some macaques are known to encode social stimuli at the level of single neurons [3–5]. Here, we presented rhesus macaques with a more ecologically relevant ToM task in which subjects could “steal” a contested grape from one of two human competitors. In six experiments, monkeys selectively retrieved the grape from an experimenter who was incapable of seeing the grape rather than an experimenter who was visually aware. These results suggest that rhesus macaques possess an essential component of ToM: the ability to deduce what others perceive on the basis of where they are looking. These results converge with new findings illustrating the importance of competitive paradigms in apes [6]. Moreover, they raise the possibility that, in primates, cortical cells thought to encode where others are looking [7] may encode what those individuals see as well.

Results and Discussion

In a number of pioneering studies, neurophysiologists investigating macaque temporal cortex have identified cells that represent the direction of other individuals' gazes in enough detail to determine where those individuals are looking (and potentially what they see) [7, 8]. To date, however, the specific cognitive abilities subserved by these gaze-sensitive neurons remain unclear [9]. Although macaques spontaneously attend to and follow the gaze of others [10–14], they appear unable to use this information to reason about what other individuals see and know [15]. Therefore, gaze-sensitive cells may only support the capacity to respond to the direction of other individuals' gazes without necessarily representing their mental states (i.e., what they see), a capacity that is importantly different from our own species's ToM abilities.

Here, we provide the first behavioral evidence that rhesus macaques detect more than simply where another individual's eyes are oriented. In particular, we suggest that rhesus macaques are able to use another individual's

direction of gaze to determine what that individual can and cannot see. Our work builds on the recent insight that primates will most likely exhibit sophisticated ToM abilities in experimental scenarios that mimic the natural situations for which these abilities have evolved—namely, competitive foraging situations [16, 17]. Despite robust failures in previous ToM tasks [1–2, 18], chimpanzees have succeeded in reasoning about another individual's potential visual knowledge when vying for food in competitive interactions [6, 19]. Results like these raise the possibility that macaques (as well as other monkey species [20]) may possess a similar ability and, therefore, that gaze-sensitive neurons in macaque cortex may support sophisticated ToM reasoning.

In the present six experiments, we ask whether free-ranging rhesus monkeys from the Cayo Santiago population reason about what a human competitor can and cannot see. The monkeys in this population are naturally curious about the foods that human experimenters bring to the island [21] and occasionally try to obtain these foods, even though they are also somewhat apprehensive of getting close to humans. We presented subjects with the opportunity to take a grape from one of two human “competitors” (Figure 1). We reasoned that subjects should be motivated to take the grape only when they can do so without being detected. We thus predicted that subjects would spontaneously use information about where the two competitors were looking when deciding which of the two competitors to approach. In particular, subjects should selectively approach the competitor whose gaze is directed away from the contested grape or whose view of the grape is otherwise occluded. Success in this situation involves more than mere gaze following; subjects must spontaneously use information about the direction of an individual's gaze to make a task-relevant decision.

In the first experiment, we allowed subjects to choose between two competitors who differed in their overall body orientation: one with his entire body facing away from the grape, the other facing toward the grape. Subjects reliably approached the competitor whose back was facing the contested grape (binomial probability: $p < 0.0001$; Figure 1A). This finding suggests that macaques will take into account differences in the competitors' positions when choosing which grape to approach and, moreover, that they do so partly on the basis of what each individual can see. We then explored whether this result was simply due to a general avoidance of the experimenter who was facing forward. In experiment two, the competitors placed their platforms down to their sides, rather than in front of them. Subjects therefore had to choose between a competitor who was facing 90° to the side and staring at the platform or to approach a competitor who was facing 90° to the side but with his back to the platform. Even though both experimenters revealed only their profile in this experiment, subjects reliably approached the experimenter with his back to the platform rather than the one with

*Correspondence: jonathan.flombaum@yale.edu

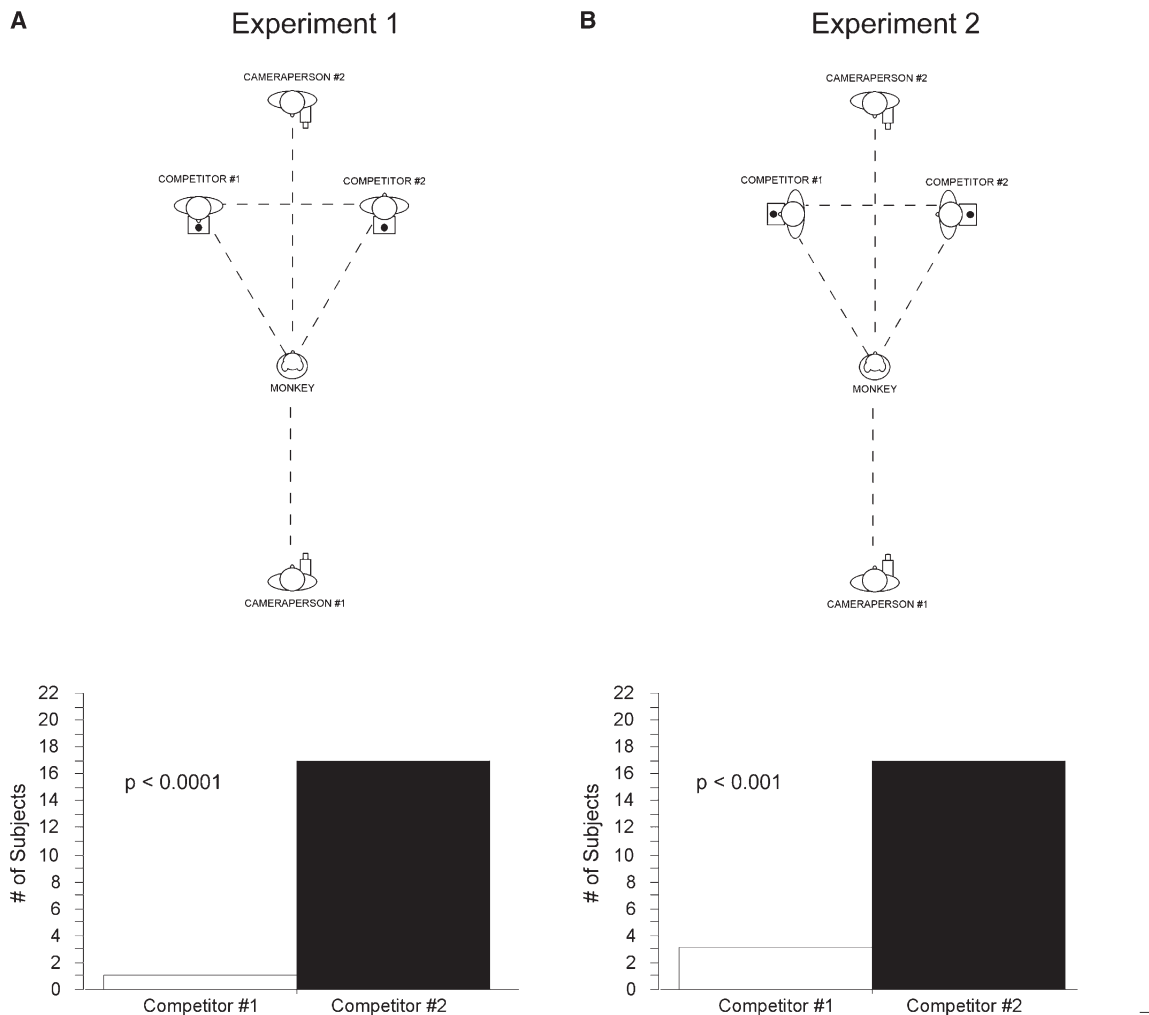


Figure 1. The Experimental Setup and Results of Experiments One (A) and Two (B)
Subjects were allowed to approach the grape in front of one of the two competitors while two camerapersons filmed them.

his front to the platform (experiment two: $p < 0.001$; Figure 1B).

We next explored whether macaques also take into account more subtle cues to where a person is looking. In the next two studies, subjects selectively retrieved the grape from a competitor whose head and eyes were oriented 90° away (experiment three: $p < 0.0001$; Figure 2A) and also from a competitor whose eyes alone were oriented 45° to the side (experiment four: $p = 0.008$; Figure 2B). Taken together, these four experiments demonstrate that rhesus monkeys spontaneously and successfully employ information about the competitors' eyes when deciding which grape to approach. Even without training, our subjects knew to attend to the specific feature of the competitors' posture that determined what they could and could not see: the direction of their eyes. Although this result differs from previous findings with macaques in noncompetitive behavioral situations [15], it is consistent with neurophysiological work suggesting that macaques have cells devoted to detecting (and therefore potentially using) gaze direction irrespective of head and body orientation [7].

In the final two experiments, we explored a slightly

different question about rhesus monkeys' knowledge of visual perception. Specifically, we considered whether monkeys take into account the presence of a visual barrier when competing with human experimenters for contested grapes. Experiment four proceeded as the previous experiments did except that both competitors in this experiment carried a large opaque barrier (20×80 cm). One competitor held this barrier horizontally in front of his body. Although the barrier blocked a large portion of the competitor's body, it did not block his eyes. The other competitor held the barrier vertically in front of his body so that it blocked his face and eyes. Unlike the horizontal barrier, this vertical barrier served as a *visual occluder*, preventing this competitor from seeing the grape. We predicted that subjects should selectively approach the competitor with his face and eyes blocked if and only if they understand the nature of visual occlusion. As predicted, subjects reliably approached the grape in front of the experimenter whose eyes were blocked by the vertical barrier ($p < 0.01$; Figure 2C). Subjects show a similar effect with smaller visual barriers—they selectively approach an experimenter with a small (6×20 cm) barrier in front of his

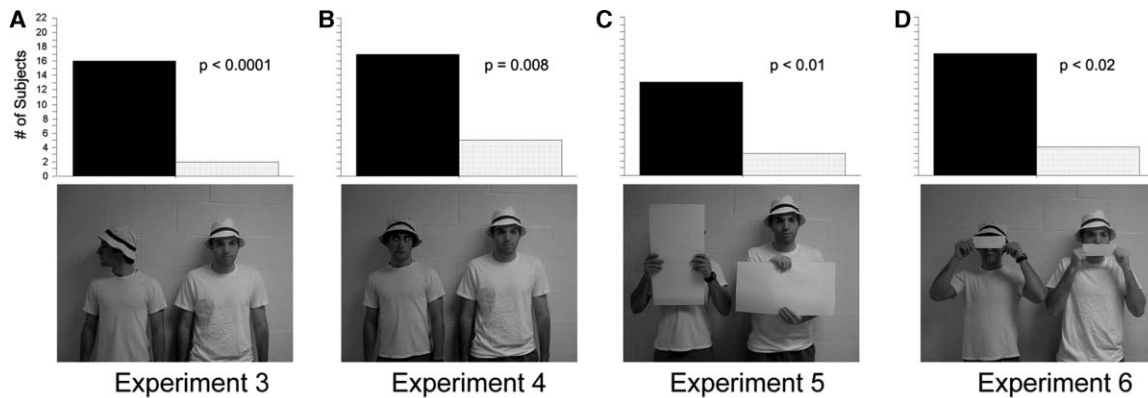


Figure 2. Results of Experiments Three through Six (A–D)

In each experiment, significantly more subjects (p values reflect binomial probabilities) retrieved grapes from the competitor who was unable to see them rather than the one who could.

eyes instead of one with an identical barrier in front of his mouth (experiment five: $p < 0.002$; Figure 2D).

Conclusions

Across the six experiments presented above, rhesus monkeys correctly use information about what a competitor can and cannot see in order to retrieve a contested piece of food. Because the monkeys in these experiments must selectively avoid the experimenter who could potentially see the contested food item, it is difficult to interpret these results in terms of a simple mechanism for responding to the gaze of another individual without representing that individual's perceptions. The animals in these studies needed to first represent what the two competitors could and could not see, and then to make a choice, based on this knowledge, to approach the experimenter who was not visually aware. Consequently, beyond demonstrating that rhesus monkeys are *sensitive* to eye-gaze direction, these experiments constitute the first evidence that a non-ape species spontaneously reasons about another individual's *visual perception*.

To anyone familiar with rhesus monkeys' natural behavior, our subjects' performance in these studies may appear unsurprising. However, our subjects' performance is actually quite remarkable when considered in light of previous experimental studies of ToM in primates. In these previous studies, rhesus macaques and other primates have systematically failed to use information about visual perception. Specifically, in object-choice paradigms, wherein an experimenter attempts to communicate the location of a hidden food by either orienting toward its location or gesturing at it, monkeys and apes have been unable to correctly read and use eye gaze in the absence of explicit training ([15, 22–29]; but see [30] for successes in dogs). We hypothesize that our paradigm better approximates the normal social conditions in which primates naturally use visual perception and therefore is a better method for eliciting this type of reasoning in a controlled experimental context [16–17, 31]. Several recent studies have successfully applied this logic to developing paradigms for studying mental-state attribution in chimpanzees [6, 19, 32–33].

Our experiments add to this growing literature by extending this approach to a non-ape species—in particular, one used as a neuroscientific model. In addition, the methods developed here bear several advantages for the further study of ToM abilities in primates. First, these methods allow for study of naive populations and with the use of only a single experimental trial per individual. Consequently, they reflect abilities that are available to the subject spontaneously and in the absence of training. Further, by employing human competitors as opposed to conspecifics, these methods afford an opportunity to manipulate very subtle and specific cues to visual knowledge (e.g., holding a barrier over the eyes versus holding a barrier in front of the mouth) and, thereby, the ability to programmatically dissect the cognitive mechanisms of mental-state attribution.

There is, however, at least one deflationary account of these results: Subjects may have performed successfully without reasoning about the mental states of their human competitors simply by, as a rule, avoiding the experimenter looking forward. It is worth considering such an account carefully, in various incarnations, in part because it leads to some introspection about the nature of our own ToM abilities: Would a human participant presented with a similar problem solve this task by doing more than merely avoiding the experimenter looking forward? In its simplest form, such an account of our results might appeal to the fact that rhesus monkeys, as well as many other primates, view direct gaze as threatening [35]. Perhaps, then, subjects avoided the experimenter facing straight ahead simply because that individual looked more threatening. Such an account seems unlikely in light of the findings in experiments four through six; in these studies, both competitors faced directly forward, and only a slight deviation of their eyes, or the presence of an occluder blocking their eyes, distinguished which of the two competitors could and could not see. Moreover, in experiment two, both competitors stood sideways in relation to the subject—that is, with their profile facing the monkey. Even though neither competitor faced forward, subjects nonetheless approached only the competitor who was not looking at the food. Subjects therefore choose on the basis of what each competitor can and cannot see, even when their

overall demeanor is equally threatening. For these reasons, we conclude that subjects did not show successful performance simply because they found one of the postures more threatening than the other.

It is still possible, however, that subjects succeeded in these experiments not because they were more or less threatened, but also not through mental-state attribution per se. Instead, subjects may have succeeded through the application of a simple nonmentalistic rule: Avoid the experimenter whose posture makes him more likely to react to your approach [17–18, 36]. Note that a rule such as this one could potentially explain any ToM-like behavior without the explicit representation of the mental state of another individual. For example, in experiment one, the monkeys may approach the experimenter whose back is facing them not by representing “His back is toward me; therefore, he cannot see me or the grape” but by representing “His back is toward me; therefore, he probably will not respond as I approach.” Indeed, some researchers argue that no experiments like the ones presented here could ever unconfound these two kinds of interpretations [36].

We would like to argue that, in this context, applying such a rule successfully is precisely the point and, indeed, qualifies as reasoning about the perceptions of others. This is because such rules *should not apply* successfully in all contexts. Avoiding the experimenter looking forward works in a competitive foraging situation, but the same rule would not work for choosing among potential mating partners, for example, where an organism would be ill-served by a rule to always approach conspecifics who could not see them or will probably not respond to them. Thus, it is the process of applying the correct rule in the correct situation that qualifies the behaviors observed here as involving a ToM. The monkeys that we tested had to first understand that where competitors look constrains what they can potentially see in order to then conclude that the competitor looking straight ahead is the one to avoid—it is, after all, the fact that one competitor cannot see the monkey and the grape in front of him that renders him unlikely to react to the monkey’s approach. In experiments four and six, moreover, the monkeys that we tested revealed an appreciation of how one’s eyes, specifically, are the most relevant factors in determining which competitor is best to avoid. It is not clear, then, how meaningful the distinction becomes between representing “His eyes render *him* *unable* to see the grape” in comparison to representing “his eyes render him *unlikely* to approach the grape.” Of course, a human participating as a subject in these experiments could certainly represent the situation in either way, and would probably do much more. In addition to representing the content of a competitor’s perceptions, a human might use the position of a competitor’s eyes to determine what the competitor plans on doing or what he or she desires, or even to evaluate the accuracy of his or her knowledge. However, none of these sophisticated processes could occur unless the organism first has an understanding of how other individuals’ direction of eye gaze constrains what they see, an ability that we appear to share with rhesus monkeys.

By identifying mechanisms in rhesus monkeys that

not only detect eye-gaze orientation in others but also use this information in a socially relevant way, these experiments begin to forge a link between the cognitive systems responsible for social reasoning and their neural substrates. Our data suggest that this species not only identifies *where* other individuals are looking, but also *what they see*. Although reasoning about the perceptions of others is only one form of mental-state attribution and thus only one component of the broad suite of mechanisms involved in reasoning about other minds, it appears to be a form of reasoning available spontaneously to the very species used in neurophysiological investigations of social cognition. With behavioral methods that single out these abilities and an understanding of potential neurophysiological substrates, we are poised to begin teasing apart subtly different aspects of ToM, both cognitively and neurally, in an animal model.

One outstanding question in the study of human ToM abilities, for instance, concerns the role that the amygdala plays in reasoning about perception and gaze [37]. The amygdala is known to show sensitivity to the direction of another individual’s gaze [38], but it tends to respond to gaze information with a slightly longer latency than other areas, such as the superior temporal sulcus (STS) [39]. Moreover, it is known that damage to the amygdala results in a generalized impairment in reasoning about both visual perception and mental states [40, 41]. Because the amygdala is known to bind emotional content with sensory information, some have hypothesized that the amygdala may provide the critical link in reasoning about what others see in addition to where they are looking [3, 4]. That is, perhaps the STS is largely responsible for analyzing where another individual’s eyes are spatially “pointing,” independent of the orientation of the rest of their body, whereas the amygdala may instead be responsible for using this information to figure out what that individual sees [9]. Our behavioral paradigm is sensitive enough to investigate this hypothesis if it is used in conjunction with lesioning techniques, and this type of cellular-level cognitive neuroscience could potentially help us to better understand fundamental social-cognitive mechanisms that appear to be disrupted in disorders such as autism and schizophrenia.

The success of the experiments presented here is surely due in part to the fact that they mimic the socio-cognitive problems that primates naturally face in the wild. Specifically, they explore what primates know about the eyes of others through competitive foraging situations. Such naturalistic paradigms have already provided comparative psychologists with a better window on primate sociocognitive abilities by demonstrating that primates possess cognitive capacities that were once thought to be unique to the human species [17]. We propose that a similar approach will eventually provide neuroscientists with a clearer window on the neural structure of ToM. In addition to providing a primate model for ToM systems, a more ecological approach may yield insight into how human sociocognitive systems have evolved and, in particular, the evolutionary contexts for which our human ToM was designed [42]. Our hope is that evolutionary insights into the function of these systems may serve to constrain hypotheses about how these systems are organized at a neural level.

Experimental Procedures

Subjects

We tested free-ranging rhesus monkeys, *Macaca mulatta*, living on the island of Cayo Santiago. The Cayo Santiago field site is run and maintained by the Caribbean Primate Research Center and the University of Puerto Rico. The current population consists of 1000 individuals divided into approximately eight social groups. Each subject has a distinctive set of ear notches and chest tattoos and therefore can be easily identified. Cayo Santiago staff provision subjects with monkey chow at three feeding stations; subjects also eat a variety of foods on the island; these foods include leaves, flowers, small plants, and soil. Subjects also have occasional access to the food that humans consume on the island [21]. The staff provides subjects with ad libitum access to water at a number of sources. The individuals in this population have served as research subjects for nearly 70 years. For this reason, subjects are well-habituated to human observers. In addition, we have successfully tested this population on similar cognitive experiments for the past 10 years (e.g., [21]).

Apparatus and Procedure

Four experimenters performed the experiments. The first two acted as the competitors (competitor one and competitor two), presenting subjects with grapes mounted on square foamcore platforms (200 cm²). The two male experimenters who served as competitors wore the same clothes (a white shirt, green shorts, and a white hat) and were matched for approximate height and build. The other two experimenters filmed the interaction (cameraperson one and cameraperson two) with Sony Digital-8 cameras. Cameraperson two also served as the coordinator, verbally instructing the competitors throughout the presentation. These verbal instructions served to synchronize the timing of competitors' movements throughout the presentation.

As in previous studies [21], experimenters chose subjects opportunistically, selecting animals that were seated alone in a clear area. Cameraperson one approached the subject from behind and filmed the actions of the competitors from approximately 3 m away. Cameraperson two and the competitors approached the subject from the front and stopped 2–3 m away. Once all experimenters were in position, cameraperson two began the presentation (see Figure 1). He first instructed the competitors to take a grape ("Take") that he was holding. The competitors then immediately took their grapes and held them up for subjects to see. At this time, cameraperson two walked 1–2 m back, so that he was 4–5 m away from the subject. Once in position, cameraperson two instructed the competitors to affix their grapes onto the platforms ("Kebab"), step 1 m to either side ("Step"), bend over and place the platforms on the ground ("Down"), and stand back up ("Up"). He then instructed the competitors to assume the final position described specifically for each experiment below ("Turn"). Once the competitors turned to their new position, cameraperson one called "Start," and subjects were given 1 min to approach one of the two grapes. Cameraperson one coded the first grape touched as the subject's choice. Subjects who failed to approach within 1 min were omitted from the final analysis. We also omitted trials in which another individual interfered with the subject's approach and those in which the subject approached before the end of the presentation. Video recordings of all sessions were digitized and scored offline by both authors.

Experiment One

Eighteen adult rhesus monkeys were successfully tested; 21 other subjects were approached by the experimenters but did not contribute to the analysis because of interference, experimenter error, previous testing, or early approach detected during offline coding. In this study, we presented subjects with a choice between a competitor whose eyes, head, and body were facing forward and one whose eyes, head, and body were facing 180° away. Each session of experiment one proceeded as described in the Apparatus and Procedure section. After the competitors had placed their platforms on the ground, cameraperson two said "Turn," and one of the two competitors turned his eyes, body, and head 180° from the platform. After the competitor completed his turn, cameraperson one called "Start" and allowed the subject 1 min to approach one of the two competitors.

Experiment Two

Twenty adult rhesus monkeys were successfully tested; 75 other subjects were approached by the experimenters but did not contribute to the analysis because of interference, experimenter error, or previous testing. This study was nearly identical to experiment one, except for the placement of the platforms and the position of the competitors. In this study, when cameraperson two called "Down," each competitor placed his platform down to his side, rather than in front of him. Therefore, from the subject's perspective, the grape platforms were not positioned between the subject and the competitors, but rather were placed to the side of the competitors. Once the platforms were placed down and cameraperson two called "Up," both competitors turned 90° in relation to the subject and, thus, faced the platforms. Cameraperson two then called "Turn," and one competitor turned 180° to the side. In this final position, the competitor that turned stood with his back toward the grape while the other stood facing his grape; note that in this position, both competitors revealed only their profile to the subject. After the competitors were in position, cameraperson one called "Start" and allowed the subject 1 min to approach one of the two competitors.

Experiment Three

Eighteen adult rhesus monkeys were tested successfully; 75 other subjects were approached but did not contribute to the analysis because of interference, experimenter error, previous testing, early approach, or disinterest. In this study, we presented subjects with a choice between a competitor whose eyes and head were facing forward and one whose eyes and head were facing 90° to the side. Experiment three proceeded as described in the Apparatus and Procedure section. After the competitors had placed their platforms on the ground, cameraperson two said "Turn," and one of the two competitors turned his head and eyes 90° from the platform. After the competitor completed his head turn, cameraperson one called "Start" and allowed the subject 1 min to approach one of the two competitors.

Experiment Four

Twenty-two adult rhesus monkeys were tested successfully; 51 other subjects were approached but did not contribute to the analysis because of interference, experimenter error, or previous testing. In this study, we presented subjects with a choice between a competitor whose eyes faced forward and one whose eyes were facing 45° to the side. Each session of experiment four proceeded as described in the Apparatus and Procedure section. After the competitors had placed their platforms on the ground, cameraperson two said "Turn," and one of the two competitors turned his eyes 45° from the platform. After the competitor's eyes were in position, cameraperson one called "Start" and allowed the subject 1 min to approach one of the two competitors.

Experiment Five

Sixteen adult rhesus monkeys were tested successfully; 37 other subjects were approached but did not contribute to the analysis because of interference, experimenter error, or previous testing. Experiment five presented subjects with a choice between a competitor holding a barrier (20 × 80 cm) horizontally in front of his body and one holding a similar barrier vertically in front of his chest and face. Experiment five proceeded as described in the Apparatus and Procedure section, with a few slight changes. After the competitors had stood up after placing their platforms on the ground, cameraperson two said "Clutch," and both competitors grabbed their barriers. After they had their barriers in hand, cameraperson two called "Turn," and both competitors turned their barriers in unison, one turning it vertically in front of his face and chest, the other turning it horizontally in front of his chest. After the competitors finished turning their barriers, cameraperson one called "Start" and allowed the subject 1 min to approach one of the two competitors.

Experiment Six

Nineteen adult rhesus monkeys were tested successfully; 44 other subjects were approached but did not contribute to the analysis because of interference, experimenter error, or previous testing. Experiment six presented subjects with a choice between a competitor holding a small barrier (6 × 20 cm) horizontally in front of his eyes and one holding a similar barrier horizontally in front of his mouth. Experiment six proceeded in the same way as experiment five. After the competitors had stood up after placing their platforms on the ground, cameraperson two said "Clutch," and both competi-

tors grabbed their barriers. After they had their barriers in hand, cameraperson two called "Turn," and each of the competitors moved their barriers in unison, one placing it horizontally in front of his eyes, the other placing it horizontally in front of his mouth. After the competitors were in position, cameraperson one called "Start" and allowed the subject 1 min to approach one of the two competitors.

Acknowledgments

This research was supported by a National Science Foundation graduate research fellowship to J.I.F. and the Yale University Moore Fund grant to L.R.S. The Cayo Santiago Field Station was supported by the National Institutes of Health (National Center for Research Resources grant CM-5-P40RR003640-13 award to the Caribbean Primate Research Center) and the University of Puerto Rico Medical Sciences Campus. The authors would like to thank David Craft, Liz Darbie, Jess Falco, Marc Florman, Venkat Lakshimanarayanan, David Lieberman, Derek Lyons, Mark Maxwell, Webb Phillips, Tamar Rudnick, Maya Shankar, and Bailey Spaulding for their help running these studies and Melissa Gerald for her help in securing the Cayo Santiago Field Station. The authors would also like to thank Geoff North and two anonymous reviewers for many helpful comments on an earlier version of the manuscript.

Received: November 8, 2004

Revised: December 21, 2004

Accepted: December 22, 2004

Published: March 8, 2005

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